Dispersal, Eviction, and Conflict in Meerkats (*Suricata suricatta*): An Evolutionarily Stable Strategy Model

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abstract: Decisions regarding immigration and emigration are crucial to understanding group dynamics in social animals, but dispersal is rarely treated in models of optimal behavior. We developed a model of evolutionarily stable dispersal and eviction strategies for a cooperative mammal, the meerkat *Suricata suricatta*. Using rank and group size as state variables, we determined state-specific probabilities that subordinate females would disperse and contrasted these with probabilities of eviction by the dominant female, based on the long-term fitness consequences of these behaviors but incorporating the potential for error. We examined whether long-term fitness considerations explain group size regulation in meerkats; whether long-term fitness considerations can lead to conflict between dominant and subordinate female group members; and under what circumstances those conflicts were likely to lead to stability, dispersal, or eviction. Our results indicated that long-term fitness considerations can explain group size regulation in meerkats. Group size distributions expected from predicted dispersal and eviction strategies matched empirical distributions most closely when emigrant survival was approximately that determined from the field study. Long-term fitness considerations may lead to conflicts between dominant and subordinate female meerkats, and eviction is the most likely result of these conflicts. Our model is computationally intensive but provides a general framework for incorporating future changes in the size of multimember cooperative breeding groups.

Keywords: cooperative breeding, ESS model, reproductive skew, social queuing.

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Among social species, decisions regarding leaving and joining social groups are crucial to understanding both group dynamics and within-group interactions. Determining the basis of these decisions has important implications for both our interpretation of social evolution and our understanding of, for example, the partitioning of reproduction between group members (the degree of reproductive skew). However, optimal decisions regarding joining and leaving groups are rarely examined in models of actual populations, prompting calls for models that focus on specific systems (Clutton-Brock 1998*a*; Johnstone 2000; Magrath and Heinsohn 2000).

Determining optimal dispersal decisions is complex, owing to the dynamic nature of social groups, which may confound attempts to assess the long-term consequences of decisions. The issue is further complicated by the interdependence of the behaviors of different group members. This interdependence requires a game-theoretic approach that assesses the optimal strategy of an animal in a given state (e.g., of age, rank, or physical condition) in relation to the optimal behaviors of conspecifics (Maynard Smith 1982). Given the computational requirements of such an approach, it is perhaps unsurprising that most theoretical models of optimal behavior within groups focus on the smallest possible groups (of only two members; e.g., Johnstone and Cant 1999; Kokko and Johnstone 1999), treat subordinates as generally identical (e.g., Reeve and Emlen 2000), or treat the decisions of subordinates as independent (e.g., Johnstone et al. 1999). Determining optimal behaviors in complex social settings is also open to the criticism that animals cannot possibly be aware of the precise decisions that their conspecifics will make or

of the exact state of their environment and the opportunities available to them.

One recent development has substantially alleviated both the problem of computational intensity and that of the assumption of omniscience. Specifically, McNamara et al. (1997) have developed a method that permits optimal behaviors to be determined while incorporating the potential for error. This not only ensures a unique solution for game-theoretic optimization, increasing the chances of determining a solution with less computational effort, but it is also more realistic. Animals will not always make the right decision, and the approach of McNamara et al. (1997) allows for this. Critically, however, the probability that an animal will make a wrong decision decreases with the cost of that decision, thus ensuring that the greater the selective pressure for correct decision making, the less often model solutions will suggest that animals will err.

In this article, we use empirical data to parameterize a model of evolutionarily stable strategies (ESS; Maynard Smith 1982) for dispersal and eviction among social mammals that we assume can disperse only once in their life. We follow earlier syntheses that assess the stability of group membership (Higashi and Yamamura 1993) by considering the evolutionary interests of more than one party. Specifically, we consider how the interests of both dominants and subordinates are affected by subordinate departures. The interests of these parties are likely to differ because relatedness between actors and their offspring is unlikely to be the same as the relatedness between actors and the offspring of others. Our approach is applicable to multimember groups and also considers the future interests of individuals.

The model is constructed with reference to the life history of the meerkat, a desert-adapted, social mongoose living in groups containing two to more than 30 members (e.g., Clutton-Brock et al. 1999*a*; Russell et al. 2002). At present, less is known about the reproductive success of males than of females of this species, and, consequently, we focus on the processes underlying female membership of groups. We use the model to address three major questions. Can long-term fitness considerations explain the emigration behavior of female meerkats and, thus, the regulation of group size? Do long-term fitness considerations lead to conflict between dominant and subordinate meerkats? What is the most likely nature of conflict over group membership, and what are the implications of this for our understanding of reproductive skew?

Methods

Study Species

The study species is described in detail elsewhere (e.g., van Staaden 1994), but here we present a brief description of some aspects relevant to this study. Meerkats are small, social mongooses, rarely exceeding 800 g in weight. They form social, matrilineal groups of from two to more than 30 individuals, typically ranging over an area of 2–5 km^2. In each group, one male and one female are socially dominant and are the parents of most of the litters born (Clutton-Brock et al. 2001*a*; Griffin et al. 2003). Subordinate females may attempt to breed in their natal group, although their offspring are often killed by the dominant female (Clutton-Brock et al. 1998; Russell et al. 2003*a*). Males never gain reproduction in their natal group but may do so by roving for short periods of time in search of subordinate females from other groups (Griffin et al. 2003). Breeding occurs primarily during the months of September to March, but births have been recorded in most months of the year (Russell et al. 2003*a*). There is no evidence of pronounced seasonal mortality (Clutton-Brock et al. 1999*b*). Pups remain below ground for much of their first month of life but can be counted between 2 and 3 weeks of age during temporary emergence (Brotherton et al. 2001; Russell et al. 2003*a*). Litter failure is rare for dominant females but common for subordinates (Clutton-Brock et al. 1998; Russell et al. 2003*a*). During their first year of life, females seldom breed or disperse, and males seldom disperse or go prospecting for females; instead, most individuals concentrate on helping (Clutton-Brock et al. 2002). Among females, immigration into other groups does not occur, and successful emigration results in the formation of a new group.

For the data used to parameterize our model, meerkats were studied on uncultivated ranchland near Vanzylsrus (25°8′S, 20°49′E) in the South African Kalahari. Details of the habitat and climate during the study period are provided elsewhere (Clutton-Brock et al. 1999*b*; Russell et al. 2002). Up to 28 groups were identified during the study period (1993–2001), but for the life-history data presented below, only data from the 14 most intensively studied groups were used. These data comprised over 240,000 meerkat days. Where necessary, means are presented with one standard error.

The Model

Currently, female reproductive success is better understood than that of males, and, hence, the model focuses on the behavior of females. We consider the decision faced by a subordinate female of rank x in group size y of whether to disperse and, similarly, the decision faced by the dominant regarding whether to evict that subordinate. Three behavioral assumptions are inherent in the model design, and we detail these before describing the model structure and, finally, the process of model parameterization.

Table 1: Notation used in the model description

Parameter	Description
C	Number of pathways by which an individual may make a stated transition
δ	Decision error parameter; see text and McNamara et al. (1997) for further details
$\Delta w_d(x, y)$	Inclusive fitness of an (x, y) individual's decision to disperse
$\Delta w_e(x, y)$	Inclusive fitness of a dominant's decision to evict an (x, y) individual
λ	Damping parameter; see text for further details
$N(D)$	Mean number of dispersers per time step
$N(E)$	Mean number of individuals evicted per time step
$P(a)$	Probability with which a group of given size (y_{int}) following deaths and dispersals will be augmented by the maturation of a young females
$P(n \rightarrow n')$	Probability of a transition from a state variable with value n to value n'
$P_D(x, y)$	Probability with which an individual in state (x, y) will disperse
$P_E(x, y)$	Probability with which a dominant will evict an individual in state (x, y)
$P_N(x, y)$	Probability of an individual in state (x, y) being present in a new group after one time step
$P_R(x, y)$	Probability of an individual in state (x, y) still being present in her group after one time step
$R(i, x)$	Coefficient of relatedness between individuals i and x
$S(d)$	Probability of an emigrant (either a disperser or an evicted animal) surviving to be present in a new group after one time step
$S(y)$	Survival of an individual in a group of y adult females, over one time step
T	Total number of time steps over which residual fitness of decisions was forecast
x	Initial rank of a focal individual
x'	Destination rank of a focal individual
y	Initial group size of a focal individual
y_{int}	Group size following all deaths and dispersals at the start of a time step but before augmentation by maturing young
y'	Destination group size of a focal individual

Model Assumptions

Linear female dominance hierarchy. Dominant tenures are long (mean, 2.0 ± 0.4 years; range, 80 days to 5.7 years; $n = 22$; the true mean may be even longer, but our data include some tenures where dominants were already in place at the start of the study). For the 14 core groups, however, 22 new instances of dominance were observed within groups of known age compositions. In six cases, only one adult female was present, and this female became the dominant; in three cases, only two adult females of equal age were present, and one went on to become the dominant. However, in the remaining 13 cases, adult females of varying ages were present. In 12 of these 13 cases, the oldest (or one of the oldest, where more than one animal of the age of the oldest subordinate was present) went on to become the dominant. Thus, it seems likely that age is a good predictor of attaining dominance in the event of a breeding vacancy.

New female dominants arise from within the group. This is also consistent with the above data on 22 changes of dominance. In each case, the replacement came from within the group.

Females do not immigrate into established groups. Of 47 females that are known to have emigrated from the core groups, none has subsequently been recorded in any previously established group.

Model Derivation

The model uses an iterative, game-theoretic approach to determine the ESS for dispersal by female meerkats in any (x, y) state (i.e., of a given rank in a given group size). These strategies (expressed as a probability of dispersal, $P_D[x, y]$, $0 \leq P_D[x, y] \leq 1$) are compared to the ESS for dominant females to evict subordinate female group members in any given (x, y) state, $P_E(x, y)$ $(0 \leq P_E[x, y] \leq 1)$. Notation used in the model description is defined in table 1.

Future reproductive success may influence the dispersal decisions of social animals that queue to inherit dominance (Kokko and Johnstone 1999). Consequently, our model assesses the consequences of dispersal (and eviction) decisions by forecasting forward over T time steps to determine the residual fitness of a decision made at the start of the entire period ($t = 0$). The basic time step used is a 3-month period (hereafter referred to as a "quarter"), as this is the approximate minimum interbirth interval (Russell et al. 2003*a*). A simple algorithm for the model is given in the appendix in the online edition of the *Amer-*

ican Naturalist, but here we detail some of the underlying theory. Our description is based on determining ESS values for $P_D(x, y)$ but is applicable to determining eviction probabilities also, except where noted. We assume that all deaths and departures take place at the start of the time step.

We begin by determining the between-state transition probabilities for a single time step, according to an individual's behavior at the start of that time step. Transitions were calculated in three different ways, depending on the actor's state and behavior. Specifically, transitions were calculated for individuals that remained in their natal group, individuals that remained in a group that they had helped to found, and individuals that emigrated to help found a new group (e.g., fig. 1). Here, we outline the process of calculating transitions for the first of these scenarios. Major differences involved in calculating transitions for the second and third scenarios are noted where appropriate and are described in more detail in the appendix.

The probability of any $(x, y) \rightarrow (x', y')$ transition depends on three components. These are as follows: $P(x \rightarrow x')$, the probability with which a new rank (x', $1 \leq x' \leq x$) is attained; $P(y \rightarrow y_{\text{int}})$, the probability that a new group size (y_{int}, $x' \leq y_{\text{int}} \leq y - x + x'$) is attained following all deaths and dispersals; and $P(a)$, the probability that the group is augmented by the maturation of a female young during the time step, such that the final group size is $y' = y_{\text{int}} + a$.

The first two of these components are dependent on the probability with which each group member is present in the group at the next time step. For a given individual in state (x, y), this probability is

$$P_R(x, y) = S(y) \times [1 - P_D(x, y)], \tag{1}$$

where $P_R(x, y)$ is the probability that she remains in the group, $S(y)$ is her probability of survival over the time step as a function of group size, and $P_D(x, y)$ is the state-specific probability that she will disperse during any time step. Where transitions were calculated for an individual that dispersed, we used $P_N(x, y)$, the probability with which an individual would be present in a newly formed group, in place of $P_R(x, y)$:

$$P_N(x, y) = S(d) \times P_D(x, y), \tag{2}$$

where $S(d)$ is the probability of surviving emigration. Note that in this case, because dominant females never disperse, the destination ranks and group sizes were bounded as $1 \leq x' \leq x - 1$ and $1 \leq y' \leq y - 1$, respectively.

Typically, for any $(x) \rightarrow (x')$ or $(y) \rightarrow (y_{\text{int}})$ transition, there are multiple combinations of individual fates by which the transition can be made. In general, the number of combinations by which an individual of rank x can attain rank x' is given by

$$C(x \rightarrow x') = \frac{(x-1)!}{(x-x')!\,(x'-1)!}. \tag{3}$$

To calculate transition probabilities, we used a readily available algorithm (available from the Combinatorial Object Server: http://www.theory.csc.uvic.ca/~cos/) to generate unique combinations of individual fates in binary code. Thus, for an $(x = 5) \rightarrow (x' = 3)$ transition, the algorithm would produce six binary strings representing the fates of the four higher-ranked individuals in terms of whether they remained in the group ($b_i = 1$) or ceased to be in the group ($b_i = 0$). These binary representations of the fates of higher-ranked individuals allowed the probability of attaining rank x' to be calculated as

$$P(x \rightarrow x') = P_R(x, y) \sum_{C(x \rightarrow x')} \left\{ \prod_{i=1 \mid b_i=1}^{x-1} P_R(i, y) \prod_{i=1 \mid b_i=0}^{x-1} [1 - P_R(i, y)] \right\}. \tag{4}$$

Given equation (4), the probability of the $(x, y) \rightarrow (x', y_{\text{int}})$ transition was given by

$$P(x, y \rightarrow x', y_{\text{int}}) = P(x \rightarrow x') \sum_{C(y \rightarrow y_{\text{int}})} \left\{ \prod_{i=x+1 \mid b_i=1}^{y} P_R(i, y) \prod_{i=x+1 \mid b_i=0}^{y} [1 - P_R(i, y)] \right\}. \tag{5}$$

Finally, there is a probability, $P(a)$, that the group will be augmented by a female offspring present in the group, which reach maturity during the time step. Note that

$$0 \leq P(a) \leq 1, \ \sum_a P(a) = 1. \tag{6}$$

To approximate the distribution of $P(a)$, we used the expected distribution of numbers of female offspring raised to maturity, given that the group's size was y_{int}. This probability distribution was determined by Monte-Carlo simulations of all component probabilities (production of emergent litters, survival, and sex ratio) as illustrated in the appendix (fig. A1). Where $a = y' - y_{\text{int}}$, the final probability of an $(x, y) \rightarrow (x', y')$ transition was given by

$$P(x, y \rightarrow x', y') = \sum_{y_{\text{int}}=x'}^{y'} P(x, y \rightarrow x', y_{\text{int}}) \times P(a). \quad (7)$$

The probabilities of transitions for individual time steps were then recursed over the T time steps in order to determine the probability, $P(x', y', t)$, with which an individual would be in any (x', y') state, t time steps in the future. Note that for $t > 0$, transition probabilities for individuals were solely dependent on their state at t and were not affected by their behavior at $t = 0$, except where this influenced values of $P(x', y', t)$.

Using values of $P(x', y', t)$ and estimates of the fitness (young raised to independence) of dominants and subordinates in groups of different sizes, the total expected fitness, $\hat{w}$, of individuals in each state was calculated according to whether they remained in the group, $\hat{w}(r)$, or dispersed from the group, $\hat{w}(d)$, at $t = 0$. Similarly, the fitness of all other group members could be calculated according to whether the focal individual stayed or dispersed. For an individual in the focal state, the inclusive fitness of a decision to leave the group, $\Delta w_d(x, y)$, was then calculated as

$$\Delta w_d(x, y) = \sum_{i=1}^{y} R(i, x)\,[\hat{w}_i(d) - \hat{w}_i(r)], \quad (8)$$

where $R(i, x)$ is the relatedness of an individual in state (i, y) to the focal state and the expected fitnesses, $\hat{w}_i(d)$ and $\hat{w}_i(r)$, are the expected direct fitnesses of individuals in state (i, y) if an individual in the focal state disperses or remains in the group, respectively. The inclusive fitness of a dominant's decision to evict a subordinate of rank x, $\Delta w_e(x, y)$, was calculated by a small modification of equation (8),

$$\Delta w_e(x, y) = \sum_{i=1}^{y} R(i, 1)\,[\hat{w}_i(d) - \hat{w}_i(r)], \quad (9)$$

where $R(i, 1)$ is the relatedness of an individual in state (i, y) to the dominant.

Dominant individuals never disperse, and hence, their probability of dispersal, $P_D(1, y)$, was always set at 0. For all other states, $P_D(x, y)$ was given an initial value of 0.5. Using these initial probabilities, the inclusive fitness of the decision to disperse by individuals in each state was calculated. For states with negative inclusive fitness, $P_D(x, y)$ was reduced, while for those with positive inclusive fitness, $P_D(x, y)$ was increased. Specifically, the new value of $P_D(x, y)$ was calculated by two steps. First, following McNamara et al. (1997), the value of $P_D(x, y)$ that represents the "best response," $B(x, y)$, to all other current strategies in the population was calculated as

$$B(x, y) = \frac{1}{1 + e^{\Delta w_d(x, y)/\delta}}. \quad (10)$$

This approach allows for some level of error in the decision making of individuals and has two key properties: it is likely to be more realistic, and it increases the potential for convergence to an ESS. The amount of error permitted by equation (10) is controlled by the parameter δ ($0 \leq \delta \leq 1$). As $\delta \rightarrow 0$, $B(x, y)$ approaches the value it would take if error was not included in the calculation. For simple, two-player games, values of $\delta < 0.1$ can greatly increase the probability of convergence to an ESS (McNamara et al. 1997). For our model, however, which simultaneously aimed to reach convergence for the strategies of over 150 different states, it is both realistic and computationally beneficial to use a higher value of δ. Preliminary simulations indicated that a value of $\delta = 0.2$ led to most scenarios converging to a solution within 500 iterations, and we therefore used this value throughout.

The second step in calculating the new value of $P_D(x, y)$ was to adjust it toward the best response. We used the formula

$$P_D(x, y) = P_D(x, y) + \lambda[B(x, y) - P_D(x, y)], \quad (11)$$

in which the parameter λ is used to damp the adjustments, avoiding the danger of nonconvergent oscillations. We used a value of $\lambda = 0.1$.

The model was reiterated until convergence was reached and the values of $P_D(x, y)$ so obtained were taken to be the ESS solution. The iterative approach was then repeated to find the equilibrium values of $P_E(x, y)$ for each state, using the slight modification detailed in equation (9).

To facilitate comparisons of the model output with field data, we also ran simple stochastic simulations to determine expected group size distributions as a function of $S(d)$. For these, groups of from two to four adult females were generated, and changes in group size were assessed on a quarterly basis. Each quarter, every individual had a state-specific probability of no longer being present in the group, $1 - P_R(x, y)$, given by

$$1 - P_R(x, y) = \max[P_D(x, y),\ P_E(x, y)] + \{1 - \max[P_D(x, y),\ P_E(x, y)]\} \times [1 - S(y)]. \quad (12)$$

Whether each individual left the group was then determined stochastically. Groups were then augmented by drawing a number of additional individuals randomly from the expected distribution of numbers of offspring

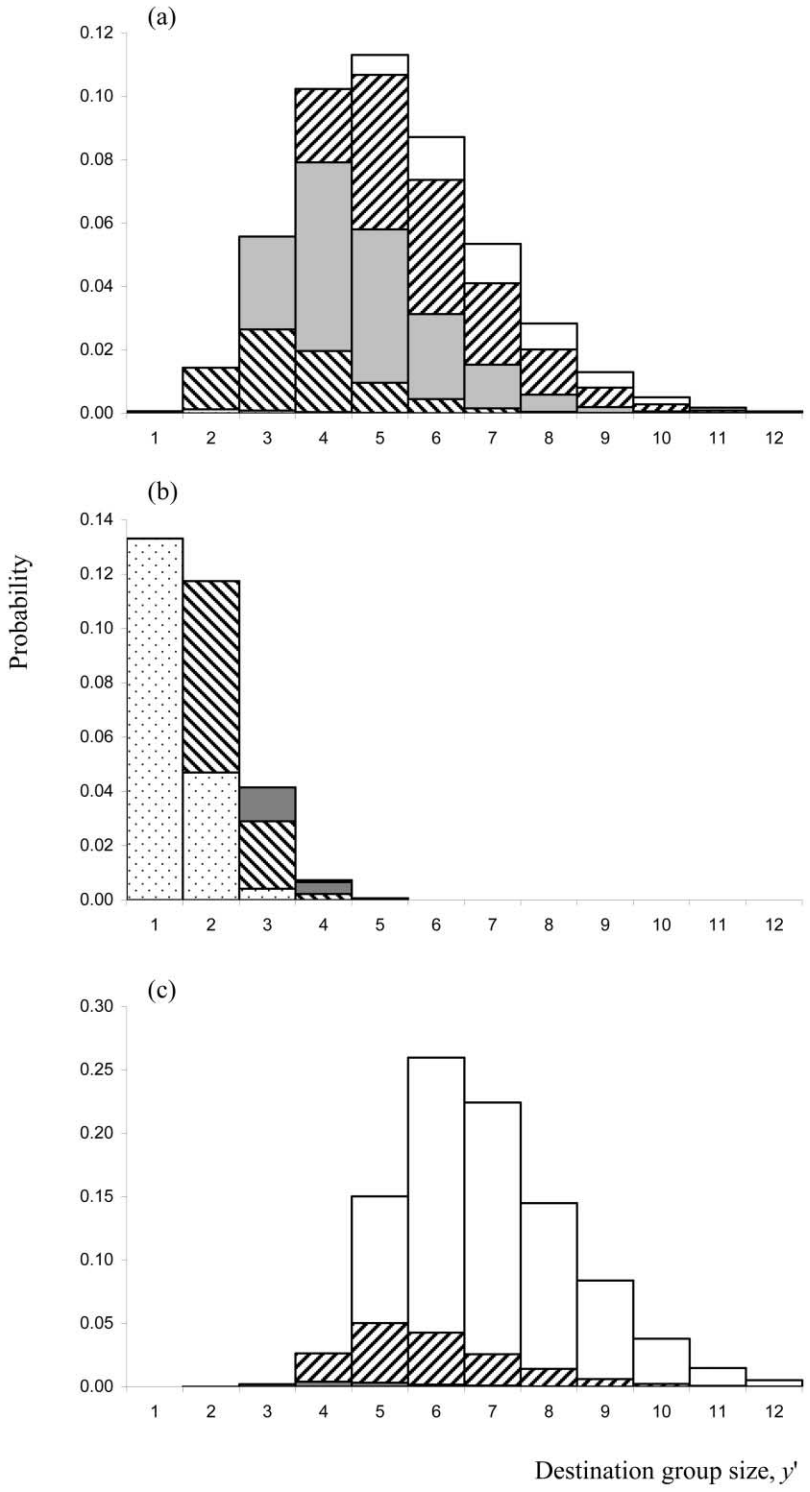

Figure 1: Sample (x', y') destination probability distributions after one time step for a female of initial state (5, 7) remaining in group (*a*), dispersing to form a new group (*b*), or remaining in a group that she helped to found (*c*). Destination ranks, x': 1 = *stippled*, 2 = *downward diagonals*, 3 = *filled*, 4 = *upward diagonals*, 5 = *unfilled*. Survival over one time step in a group with seven females, $S(7) = 0.952$. The survival of dispersers to be part of a new group, $S(d) = 0.3$. In the example shown, the probability of dispersal for dominants is 0, but for all other individuals, $P_D(x, y) = 0.5$. Notice that in *a*, the group may grow (as a result of augmentation by maturing young) or shrink (as a result of the death or dispersal of other individuals). The rank attained may vary from 1 to x. In *b*, by contrast, the destination group size will never exceed $y - 1$ because the former dominant will not disperse and no augmentation by maturing young is possible during the first time step. In *c*, the focal female's rank is unlikely to be greatly elevated because higher-ranked individuals will not disperse again. The group may be augmented by maturing young.

raised to maturity, given that the group's size was that achieved after all adult mortalities and dispersals. Group sizes were recorded each quarter for 30 time steps. This process was reiterated one million times for each of the sets of $P_D(x, y)$ and $P_E(x, y)$ associated with each probability of emigrant survival $S(d)$.

Model Parameterization

Data on survival, fecundity, and emigration behavior of meerkats have been extensively analyzed and are presented elsewhere (e.g., Clutton-Brock et al. 1999*a*, 1999*b*, 2001*b*; Russell et al. 2002, 2003*a*). We analyzed the current data set specifically to provide the parameters necessary for our dispersal model. In particular, we examined eviction and dispersal success, survival, fecundity, relatedness, and group composition. Where the term is used below, "group size" excludes pups of less than 90 days old.

Animals were assumed to have died if they disappeared before 6 months of age, if a carcass was found, or if they disappeared suddenly despite showing no dispersive tendencies (such as foraging away from the rest of the group) over previous days. That females are often temporarily evicted from their group while the dominant female is pregnant (Clutton-Brock et al. 1998) and that males commonly go prospecting (Doolan and Macdonald 1996) makes accurate identification of permanent emigration difficult. Dispersal was recorded if animals were observed alone or with another group, outside the range of their original group, and if they did not return to the source group. By this definition, most female disappearances could be attributed either to dispersal or to mortality. For males, this was less clear-cut, due to their tendency to remain with different groups for prolonged periods.

Eviction and survival of emigrants. During the study period, 134 clear instances of subordinate female eviction from the 14 core groups were recorded. The frequency with which this occurred (in relation to group size) is shown in figure 2*a*. Of the 134 evicted females, 87 returned at a later date, indicating that eviction was only a temporary measure (Clutton-Brock et al. 1998). The remaining 47 females emigrated in 17 separate events. Of these, the number of females per event varied from one to six (mode = 4). Six of these 17 emigration events (35%) are known to have resulted in the successful founding of new groups. Only three dispersers (out of the 47) are known to have died before founding a new group, but a further 27 individuals disappeared abruptly and were never seen again in or around the study area; these data accord well with more intensive observations of radio-collared dispersers (Young 2003). Long-distance dispersal cannot be ruled out for these individuals although survival over long distances and through unfamiliar ground is likely to be low. Furthermore, surviving dispersal is no guarantee that individuals will be successful in forming new groups. In caged trials, only two of five (40%) potential groups remained together when animals were removed and placed in vacant ranges. Consequently, while it is possible that some of the unaccounted individuals were successful, it is unlikely that the probability of surviving dispersal is much greater than the confirmed probability of 35%.

Survival. Daily survival rates were calculated using a standard Mayfield analysis (Mayfield 1975) for all individuals from emergence to 6 months, for all individuals of over 6 months, and for females only over 6 months (this was necessitated by the model structure). Survival rates were also analyzed for each group during each 3-month period and were related to the group size at the start of the period. Daily survival rates were as follows: 0.9983 for animals of both sexes from emergence to 6 months, 0.9995 for all individuals over 6 months old, and 0.9994 for females only over 6 months old. These equate to a mortality rate between emergence and 6 months of approximately 24% and annual mortalities for animals over 6 months old of 17% (both sexes combined) or 20% (females only). If all unaccounted disappearances were assumed to be mortality, then the combined annual mortality of animals over 6 months old would be 25%. Relationships between survival rates and group sizes are shown in figure 2*b*–2*d*.

Fecundity. For fecundity analysis, frequency of litter production and litter size may be affected in different ways (Russell et al. 2003*a*). Females are constrained by a minimum interbirth interval and typically produce no more than one litter in any 3-month period. We divided the study period into 27 periods of 3 months' duration. For each female exceeding 1 year old present in a given group for over two-thirds of a 3-month period, the average group size during that period was recorded, together with a binary score, according to whether she produced an emergent litter (1) or not (0). The effects of group, female identity, female age, group size, and female dominance status on the probability of producing an emergent litter in any 3-month period were assessed using a generalized linear mixed model (GENSTAT 5, release 4.1, Rothamsted Experimental Station, Harpenden), with female and group identities entered as random factors (Schall 1991). To assess variables affecting the size of emergent litters, we used a residual maximum likelihood model in GENSTAT, again with female and group identities fitted as random terms. We investigated whether litter sizes at emergence were influenced by female age, status, group size, and number of reproductively mature females averaged over the 2 weeks before emergence.

We identified 524 unique combinations of female, group, and period, during which 130 emergent litters were

produced. Neither individual nor group identities constituted significant random terms, and hence, a binary logistic regression was performed. This indicated that female status and group size both had significant effects on the probability of a litter emerging in any 3-month period but that these effects were not always straightforward. Per-capita probabilities of producing an emergent litter were higher for dominants than subordinates and increased with group size for dominants but decreased with group size for subordinates (fig. 2*e*). Only female status showed a significant effect on the size of emergent litters (dominants, mean = 3.95 ± 0.15; subordinates, mean = 2.90 ± 0.23; $\chi_1^2 = 15.34$, $p < .001$). The parameters derived for survival from emergence to 1 year old, as well as fecundity, were combined to predict female fitness (in terms of young raised to adulthood) in relation to group size. Relationships between annual direct fitness and group size for both dominant and subordinate females were well described by fourth-order polynomials (fig. 2*f*).

Group composition. During the study period, groups varied in size from two to 34 individuals, excluding pups of less than 90 days old. We assessed group membership on a day-by-day basis to determine the number of females per group of more than 90 days of age. Numbers of females per group varied from one to 16, and the mean was 5.9 ± 3.0 (standard deviation). The number of females as a proportion of group size was assessed as an index of group composition, using groups containing at least two females (i.e., those of interest for the purpose of modeling emigration decisions). The number of females as a proportion of group size was not significantly different from 0.5 (mean female proportion = 0.485 ± 0.009; one-sample *t*-test, not significant). For simplicity, therefore, the model was based on adult female group size with the assumption that total adult group size would be approximately twice as large.

Relatedness. Relatedness between dyads within groups was assessed on the basis of known pedigrees. More than 1,000 unique dyads were identified from the data, and relatedness could be determined in 793 cases where the origin and parentage of both individuals could be assigned with confidence. None of these dyads consisted of unrelated individuals, and the majority (65%) were full sibs or mother-daughter dyads ($r = 0.5$). Next most common (26% of dyads) were those with $r = 0.25$ (e.g., half-sibs, grandmother-granddaughter, or cousins). Overall, relatedness was higher between dominants and subordinates (mean $r = 0.47$, $n = 109$) than between subordinate pairs (mean $r = 0.39$, $n = 684$).

Results

When any set of model parameters led to a convergent solution, the output was a series of state-specific dispersal or eviction probabilities (depending on whether the interests of subordinates or dominants were considered). When group sizes of up to 18 adult females were considered, over 150 state-specific probabilities were generated. Interpretation of such a large number of probabilities is complex. However, from the state-specific probabilities, we derived the total probability with which one, two, or more individuals would disperse (or be evicted) as a function of group size. This, in turn, permitted the average number of emigrants (either dispersers, $N[D]$, or evictees, $N[E]$) to be determined, also as a function of group size. An example of this process is shown in figure 3.

Average numbers of dispersers (or individuals evicted) per quarter as a function of group size was a useful relationship by which to compare the results of different parameter combinations. In particular, we used this output to conduct a sensitivity analysis of the model predictions to the total number of time steps considered, T (fig. 4*a*). As might be expected, individuals were more likely to disperse (and thus shorten their wait for dominant status) when shorter time periods were considered. However, this willingness to disperse reduced by smaller increments as the total time considered was increased. Increases in the total time considered above 100 time steps (equivalent to 25 years) produced very little change in the model predictions, and thus, we used $T = 100$ as the standard period over which to forecast the consequences of an action. Similarly, we assessed the sensitivity of model predictions to the maximum group size considered in the model. Model output appeared to be very robust to this parameter (e.g., fig. 4*b*, 4*c*). The maximum group size observed during the field study was 16 adult females, but for flexibility in the model, we allowed for the possibility that groups could slightly exceed this size. All further results were based on assessments using a maximum group size of 18 adult females.

Predicted state-specific dispersal and eviction probabilities, together with predictions of mean numbers of dispersers and evicted individuals, were combined to develop a representation of expected dispersal and eviction behaviors, as a function of both group size, y, and survival of emigrants, $S(d)$. Specifically, the parameter space described by these factors was categorized into regions of five different behavior types: (1) stability: $N(E) < 0.5$, $N(D) < 0.5$; (2) eviction only: $P_E(x, y) > P_D(x, y)$ for all $x > 1$; (3) primarily eviction: $N(E) > N(D)$, but $P_E(x, y) > P_D(x, y)$ is not true for all $x > 1$; (4) primarily dispersal: $N(D) > N(E)$, but $P_D(x, y) > P_E(x, y)$ is not true for all $x > 1$; and (5) dispersal only: $P_D(x, y) > P_E(x, y)$ for all $x > 1$.

Regions of parameter space characterized by these five different patterns of behavior are shown in figure 5. Groups are expected to be highly stable, with few depar-

(a)
Evictions per quarter
2.5
2.0
1.5
1.0
0.5
0.0
<= 5
06-10
11-15
16-20
21-25
>= 26
(b)
Daily survival rate
1.000
0.998
0.996
0.994
0.992
0
5
10
15
20
25
30
35
Total group size
(c)
Daily survival rate
1.000
0.999
0.998
0.997
0
5
10
15
20
25
30
35
Total group size
(d)
Daily survival rate
1.000
0.999
0.998
0.997
0
5
10
15
20
25
30
35
(e)
Quarterly probability of producing an emergent litter
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
Total group size
(f)
Equivalent quarterly direct fitness of a dominant
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
2
4
6
8
10
12
14
16
18
Adult female group size
Equivalent quarterly direct fitness of a subordinate
0.30
0.25
0.20
0.15
0.10
0.05
0.00

tures, from between four and six adult females, depending on the likely survival of dispersers. This corresponds to total adult group sizes of from eight to 12 individuals, below which subordinate females would seldom be expected to disperse or be evicted. In general, figure 5 indicates that eviction is likely to be more common than dispersal throughout the broad range of parameter space, with the largest behavioral region that in which evictions outnumber dispersal. Only when the expected survival of emigrants is high is it likely that individuals would disperse voluntarily with any regularity. Furthermore, situations where the dominant female would favor retaining subordinates but the subordinates would be more likely to disperse are restricted to the single case in the top left corner of figure 5 (where group size $y = 2$, and emigrant survival $S[d] = 0.9$). Interpreting the likely patterns of behavior within the five regions distinguished in figure 5 is complex and depends on the nature of control within the group and, in particular, the physical costs of eviction to the dominant female. We return to this issue in the "Discussion."

Finally, we also used simple simulations to generate expected group size distributions, given the probabilities of dispersal and eviction determined by our ESS model. Mean and standard deviations of group size (in terms of number of females) were determined as a function of the survival of emigrants and were compared to those derived from the empirical data (fig. 6).

Discussion

Our model uses empirical data to determine ESS probabilities of dispersal for subordinate female meerkats and ESS probabilities of their eviction by dominant females. As might be expected for a detailed analysis of complex social behaviors, the results themselves are complex. Nevertheless, the model indicates that a number of general patterns of behavior might be expected among female meerkats. In particular, four findings are of interest both in the context of meerkat behavior and, more generally, to our understanding of aspects of group living and social behavior. These include that long-term fitness benefits can explain observed group sizes of meerkats, that eviction seems far more prevalent than dispersal as a mechanism for regulating group size, that situations where dominants might benefit from providing staying incentives to subordinates are unlikely to arise, and that conflict and eviction may arise even in situations where some subordinates might benefit from dispersal.

An assessment of group size based on only 14 focal groups must be treated with some caution, as mean group size may be susceptible to the size of individual groups that have been monitored for the longest periods. Nevertheless, the sizes of groups monitored during the empirical study do provide some guide to expected levels of emigration. In particular, figure 6 shows that group size distributions suggested by ESS emigration levels correspond most closely with those seen in the empirical study when the survival of emigrants is between 0.3 and 0.4. This is encouraging, given that the confirmed survival rate of emigrants from the empirical study is approximately 0.35, and suggests that meerkat group sizes can be explained by decisions made on the basis of long-term fitness considerations.

Eviction is a common phenomenon in social species and has been documented, for example, in hyenas (*Crocuta crocuta*; Holekamp et al. 1993), banded mongooses (*Mungos mungo*; Cant et al. 2001), house mice (*Mus domesticus*; Gerlach 1996), Arabian babblers (*Turdoides squamiceps*; Zahavi 1991), and splendid fairy wrens (*Malurus cyaneus*; Mulder 1995). A variety of explanations may underlie the eviction of subordinates, but our model suggests that for meerkats at least, group size regulation by the dominant in order to maximize her inclusive fitness may well underlie this behavior. Our results suggest that throughout the broad range of parameter space, and particularly for situations where survival of emigrants is relatively low ($\leq$0.4), eviction is likely to be the dominant behavior regulating group size (fig. 6). This finding corresponds well with behavioral data from the field study. While subordinate males cannot gain direct reproductive success in their own group and always disperse voluntarily, subordinate females are able to breed and inherit dominance in

Figure 2: Relationships between life-history parameters and group size derived from the field data. *a*, Eviction rate (females evicted per quarter of monitoring). Daily survival rate, *s*, for (*b*) emergence to 6 months old, (*c*) over 6 months (sexes combined), and (*d*) over 6 months (females only). Solid lines indicate best fit functions; dashed lines indicate 95% confidence intervals. Functions were chosen to maximize R^2 goodness of fit, ensuring all coefficients were significant (functions are, for *b*, $s = 0.995027 + 0.000358k - 0.000008k^2$, $R^2 = 0.4465$, $p = .0003$; for *c*, $s = 0.999663 - 0.001612/k$, $R^2 = 0.2818$, $p = .0018$; for *d*, $s = 0.999535 - 0.001063/k$, $R^2 = 0.1283$, $p = .0441$). *e*, Probability of producing an emergent litter in any 3-month period for dominants (*solid line*) and subordinates (*dashed line*). Probabilities were predicted using binary logistic regression, with significant effects of female status, group size, and the interaction between these terms. The regression function was significant ($\chi^2_3 = 190.65$, $p < .001$) and is given by $p = 1/[1 + e^{(1.594R - 0.138k + 0.097Rk - 1.389)}]$, where R is female rank (restricted to 1, dominant; or 2, all others) and k is total group size. *f*, Equivalent quarterly direct fitness of dominants (*filled circles*) and subordinates (*unfilled circles*) in relation to group size, incorporating probability of producing litters, litter size, and survival of young to adulthood.

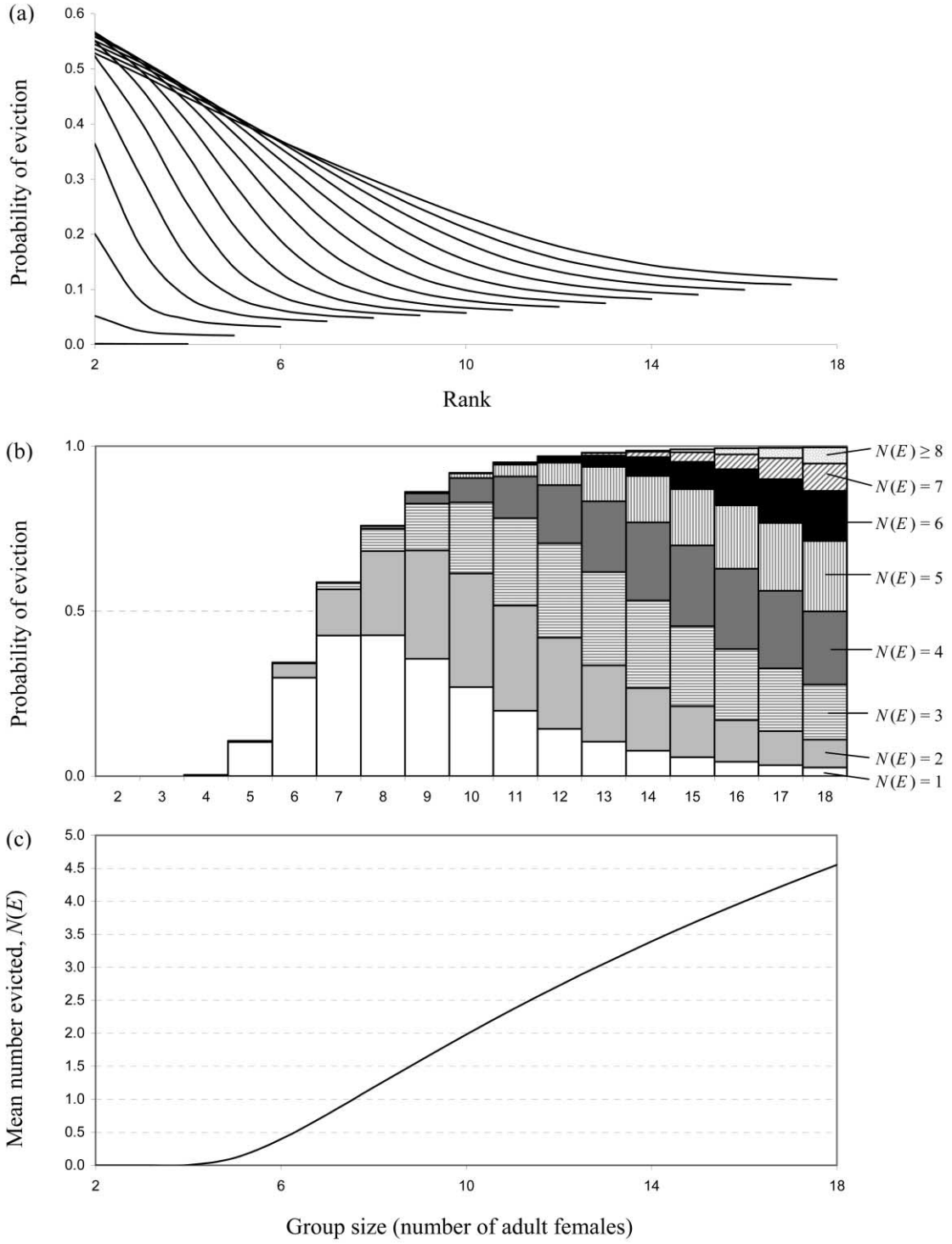

Figure 3: Sample model output when the number of time steps $T = 100$ and the survival of dispersers $S(d) = 0.3$. A convergent solution was reached after 223 iterations. *a*, Probabilities with which females of given rank in a given group size will be evicted by the dominant during any time step. Each line represents a group size (evident from the terminal point on the line). Notice that eviction probabilities for each rank generally increase as group size increases. *b*, Probabilities with which a given number of subordinates will be evicted by the dominant during any time step, as a function of group size. Numbers evicted, $N(E)$: 1 = *unfilled*, 2 = *light gray fill*, 3 = *horizontal hatching*, 4 = *dark gray fill*, 5 = *vertical hatching*, 6 = *black fill*, 7 = *diagonal hatching*, 8 or more = *stippled*. Notice that as group sizes become larger, the probability with which multiple individuals will be evicted increases. *c*, Average number of individuals evicted per time step, as a function of group size. Notice that in this scenario, eviction is likely to be extremely rare (less than 0.5 individuals per quarter on average) from groups of less than six adult females (corresponding to a group size of 12 adults).

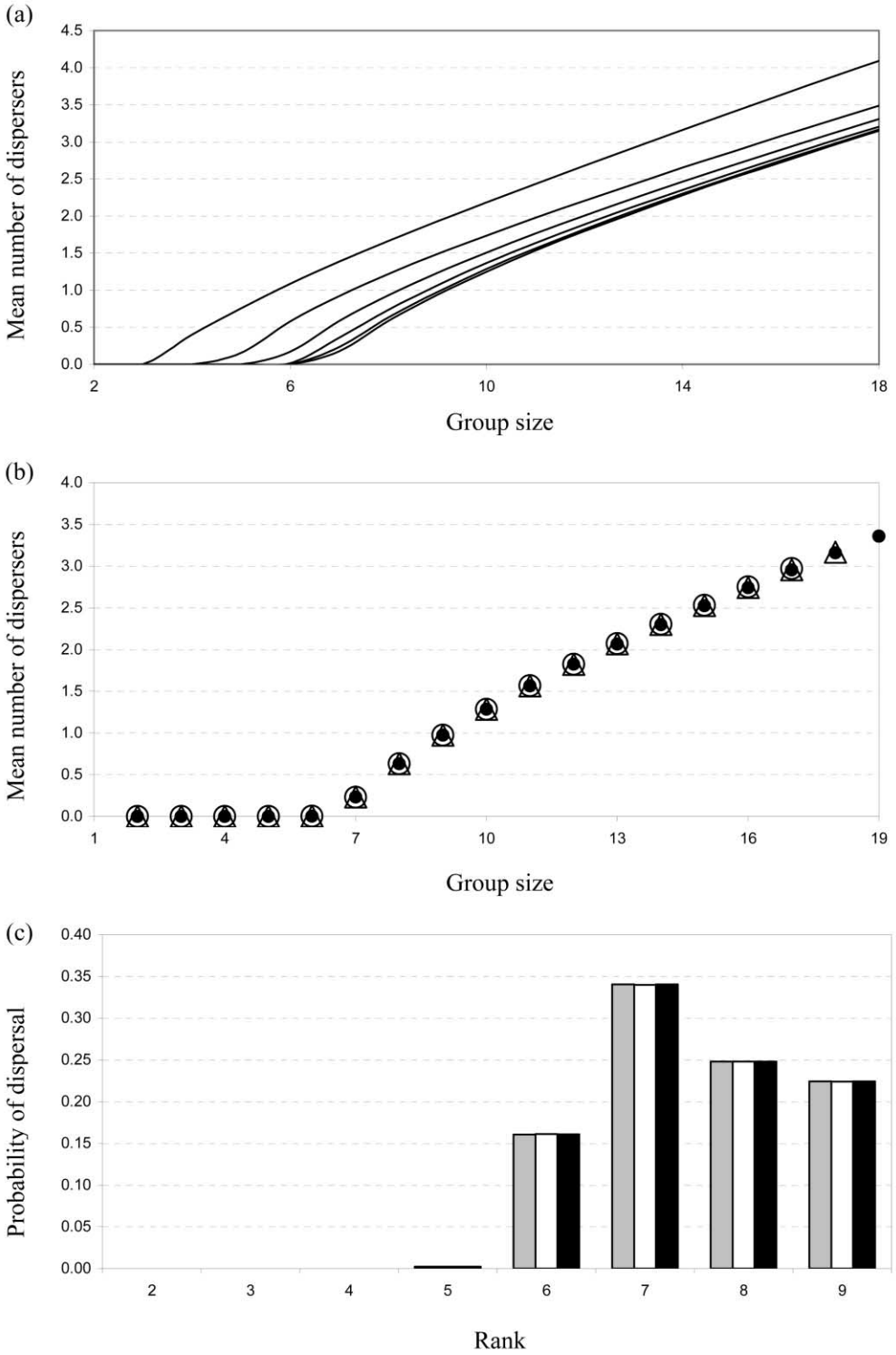

Figure 4: *a*, Sensitivity of model output to total numbers of time steps, T, over which the consequences of a decision was forecast. The lines indicate mean numbers of dispersers per quarter as a function of group size. Lines are (from left to right) $T = 20$, $T = 40$, $T = 60$, $T = 80$, $T = 100$, $T = 120$. Notice that dispersal becomes less common as T increases but that the differences between model outputs for successive increases of T become smaller. For this analysis, survival of dispersers $S(d) = 0.3$. *b*, Sensitivity of model output to the maximum group size (Y_{max}) permitted within the model. The data are mean numbers of dispersers per quarter as a function of group size when $S(d) = 0.3$: *open circles*, $Y_{max} = 17$; *open triangles*, $Y_{max} = 18$; *filled circles*, $Y_{max} = 19$. *c*, Example of state-specific dispersal probabilities when Y_{max} was varied. The data are dispersal probabilities of subordinate ranks when group size $y = 9$ and survival of dispersers $S(d) = 0.3$: *gray bars*, $Y_{max} = 17$; *unfilled bars*, $Y_{max} = 18$; *black bars*, $Y_{max} = 19$.

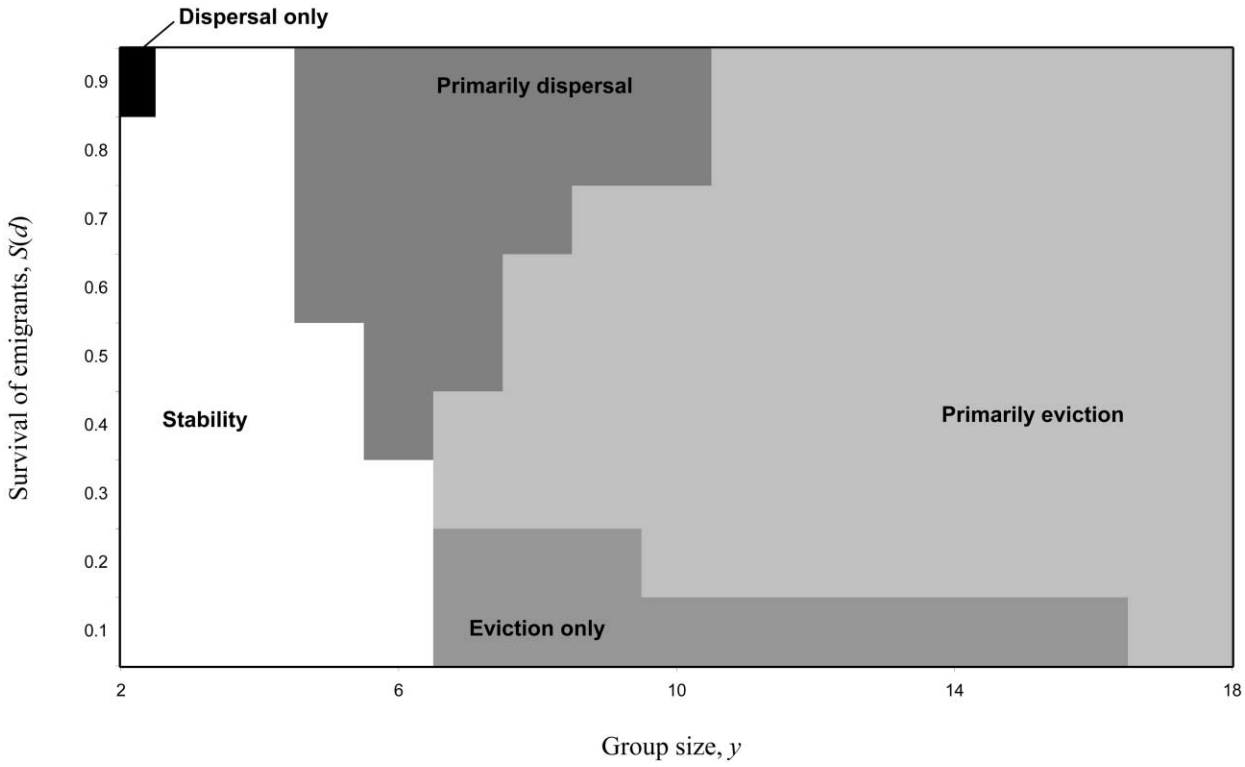

Figure 5: Regions of parameter space corresponding to the five behavioral types described in the main text. Notice that stability becomes less and dispersal becomes more likely as the survival of departing animals increases. Maximum group size $Y_{max} = 18$, and total number of time steps $T = 100$.

their natal group, and observations suggest that they disperse only when evicted.

The occurrence of eviction at relatively low group sizes (less than 10 individuals) has, in the past, seemed surprising, especially given the higher survival of young in larger groups (more than 20 individuals). Evictions can often be explained as a short-term mechanism, aimed at preventing subordinate females from breeding (at the expense of resources for the dominant's own offspring) and avoiding infanticide (Clutton-Brock et al. 1998; Young 2003). However, our results also suggest that when the dominant may make errors, evictions from even relatively small groups may sometimes occur (e.g., fig. 3*c*) for reasons other than these short-term considerations.

Groups of social animals range from egalitarian, with low levels of reproductive skew (e.g., lions, *Panthera leo*; Packer et al. 2001), to despotic, with high reproductive skew (e.g., Damaraland molerats, *Cryptomys damarensis*; Bennett et al. 1996). A multitude of theoretical models has been published, seeking to explain this variation between species in terms of ecological, social, and genetic factors. One class of these models is typified by the optimal skew model of Reeve and Ratnieks (1993). The optimal skew approach suggests that where larger group size is beneficial to dominants, subordinate reproduction may be tolerated in order to encourage subordinates to remain in the group. This idea led to considerable controversy between the competing theories of such "concessions" as explanations of subordinate reproduction versus the more parsimonious explanation that dominants simply lack complete control over the breeding behavior of subordinates (e.g., Clutton-Brock 1998*a*, 1998*b*; Emlen et al. 1998). Owing to the dearth of suitable data, empirical tests of this controversy are rare, and interpreting the merits of competing models has proven difficult (Johnstone 2000). Our model suggests that for meerkats at least, situations in which dominant animals would benefit from ceding additional reproduction to subordinates in order to persuade them to stay are extremely unlikely (fig. 5). Rather, the small amounts of subordinate reproduction that occur are likely to result for one of the following reasons: (1) because a small amount of subordinate reproduction does not limit reproduction by dominants or is cheaper for dominants than producing more of their own young (Cant and Johnstone 1999); given the extent of dominant investment in harassment of potential competing breeders within the

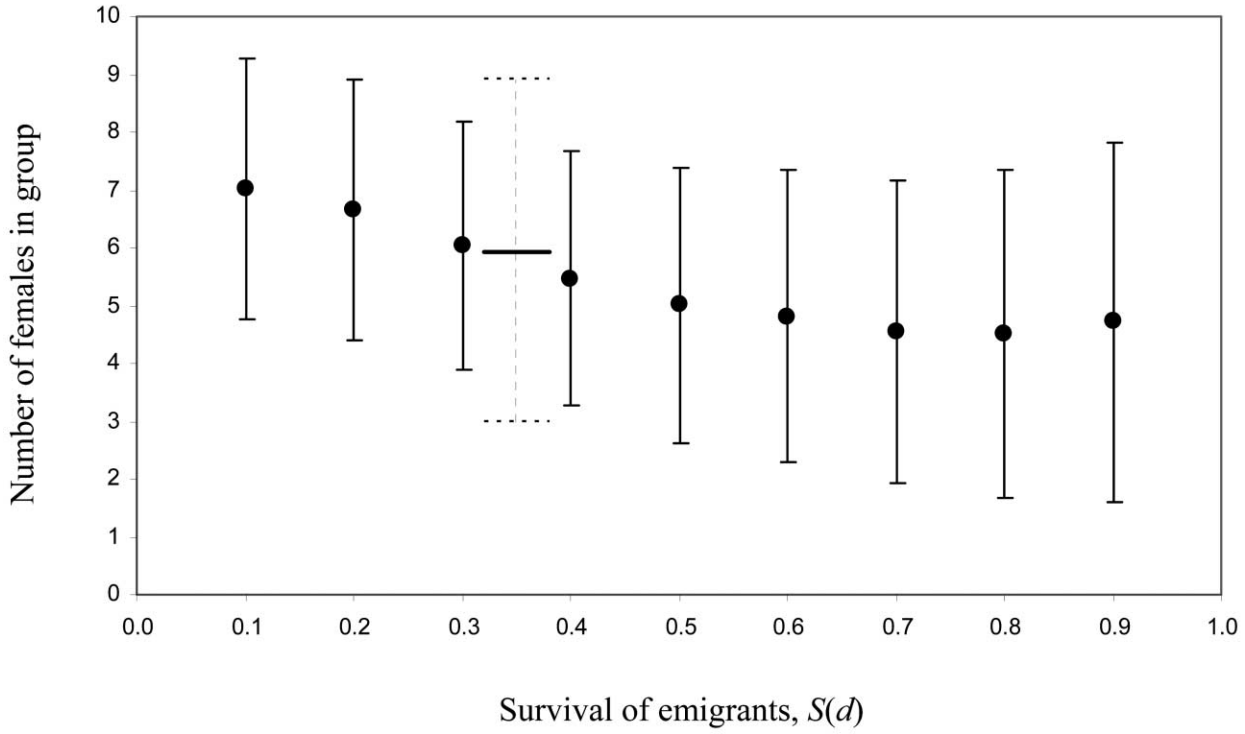

Figure 6: Group size distributions (mean, *filled circles*; standard deviation [SD], *error bars*) predicted by simple simulations of group size variation based on the evolutionarily stable strategies values of $P_D(x, y)$ and $P_E(x, y)$. Group sizes seen in the empirical study are indicated by mean (*solid line*) ± 1 SD (*dashed lines*) for the approximate value of emigrant survival, $S(d)$, indicated by the field data.

group and infanticide of competing litters (Clutton-Brock et al. 1998), this explanation is unlikely to apply under most circumstances. (2) because the dominant does not have full control over subordinate reproduction, either because eviction is costly to the dominant and, therefore, subordinates can afford to "steal" some reproduction without making their eviction worthwhile (Johnstone and Cant 1999) or because securing all reproduction in the group requires more effort than dominants are willing to expend (Clutton-Brock 1998*a*; Reeve et al. 1998).

We have noted that some aspects of our results are more difficult to interpret. In particular, these include regions of parameter space in which both evictions and dispersal are possible (although one or the other is likely to be more common in numerical terms). In these areas, whether some individuals would be evicted (reducing the probability that remaining individuals would disperse) or disperse voluntarily (reducing others' probabilities of eviction) would depend on the nature of control within the group and the extent to which subordinates are aware of likely evictions by their dominant.

It would be dangerous to read too much into the individual probabilities of dispersal and eviction predicted by our model. Specific patterns of dispersal and eviction would likely be sensitive to group composition and patterns of relatedness. Moreover, there are currently too few data to determine whether the survival of emigrant meerkats varies with their age or rank. That no female of less than 1 year has been observed to emigrate, however, suggests that for these individuals the probability of surviving emigration is likely close to 0. Similarly, we might expect that the probability of older animals (that have eluded predation for longer) surviving emigration might be expected to be higher than that for younger animals. The relationship between number of emigrants and success is also unknown at present. Low-ranking subordinates may accept subordination in a newly formed group if by moving, they increase their rank and, thus, their prospects for territory inheritance (although the costs of helping in a small, newly formed group will be high; Russell et al. 2003*b*). If the relationship between number of dispersers and probability of success were known, it would be useful to incorporate this into the model. Data currently being analyzed may well permit such developments (A. J. Young and T. H. Clutton-Brock, unpublished data).

Finally, our model is designed to assess decisions made

on the basis of mean expectations of fitness, measured as the number of young raised to independence. Two alternative formulations are possible, which may well affect the model results. First, it may be preferable to use state-dependent reproductive values (Houston and McNamara 1999) instead of young raised to independence. State-dependent reproductive values allow for future changes in population size and the consequent changes in the value of having offspring now as opposed to later. Due to a lack of data on density-dependent constraints on population trajectories, we modeled opportunities for dispersers as a constant, with the result that expected population size will not affect the value of offspring under our model formulation. State-dependent reproductive values also take account of the state into which offspring are born. For example, females may be more likely to disperse if by doing so, their offspring are likely to be born into a smaller group (and therefore be of higher rank) than if they remain in their current group. This formulation would greatly increase the computational complexity of the model. Furthermore, given both the potential for error in decision making and the speed at which group sizes can increase, it seems unlikely that this change would greatly affect the model results. As a result, we chose to use the simpler formulation of young raised to independence as a proxy for fitness. A second alternative formulation (related to the previous point) arises because environmental stochasticity can introduce major changes in selection pressures that make analyses of mean trajectories misleading. Consequently, individuals may adapt their behavior to variability in the environment (Benton and Grant 1996), worst-case scenarios (Orzack and Tuljapurkar 2001), or some other form of average. Our model is adaptable to alternative formulations such as these, and it would be interesting to determine their consequences for group size regulation and intragroup conflict.

ESS models to determine optimal strategies simultaneously for large numbers of interdependent states are rarely attempted due to the intensive computation required. Our model provides a framework by which ESSs can be derived for individuals in multimember groups of social species, taking account of the long-term consequences of decisions. The assumption of decision error is likely to be more realistic than perfect optimization and increases the stochasticity to which group sizes are subject, above that expected from stochastic birth and death events. This suggests a broader distribution of possible group sizes than would be expected under conditions of perfect optimization and helps to explain the variety of group sizes observed in reality. ESS dispersal and eviction probabilities determined by our model produce group size distributions in line with those seen in the empirical study, especially when emigrant survival is approximately that recorded in the field. This suggests that long-term fitness considerations may well explain group size regulation in meerkats. Our model also suggests that regulation is most likely to depend on eviction of subordinates by dominants, adding support to our interpretation of observed behaviors.

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